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Article

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Temporal variation in cave bear (*Ursus spelaeus*) dentition: the stratigraphic sequence of Scladina Cave, Belgium

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Abstract

The supposed herbivorous cave bear (*Ursus spelaeus*) occupied Europe throughout the Quaternary. Being subject to large spatial variation has led to the intensive study on its geographical polymorphism, generating debates on sub-speciation. However, temporal morphological information on the species is somewhat lacking. Here, we apply geometric morphometrics (GMM) technique to investigate temporal morphological variation in molar size and shape of *Ursus spelaeus* from different chronostratigraphic sediment units in a geographically confined site (Scladina Cave, Belgium), covering approximately 100,000 years.

Our findings show significant morphological variation between groups analysed in both size and shape. M^2 dentition shows a chronological size increase with PCA plots visually expressing differences in all groups, relating to a buccolingual expansion and an increase of the talonid masticatory platform through time. Reduction in the M^1 is also shown, possibly to maintain biomechanical performance of dentition for effective mastication, more so in groups relating to the latter stages of the Quaternary.

Findings suggest a rapid response to climatic factors constraining consumable food sources, with GMM offering a promising analytical approach in understanding the palaeobiology, palaeoecology and morphological variation in extinct and extant fossil mammals.

Keywords: Teeth; Geometric morphometrics; morphology; Quaternary; climatic adaptation

1. Introduction

The Quaternary was characterised by multiple glacial and interglacial periods resulting in fluctuations of warmer and colder climates across the globe (Dansgaard et al., 1982; Johnsen et al., 1992; Rasmussen et al., 2014). Controversial evidence for the impact of such climatic cycles on mammalian speciation and extinction rate has been presented (Lister, 2004; Barnosky, 2005; Sandom et al., 2014) and, depending on the species, population morphological responses remain, to some extent, questionable (e.g., Dayan et al., 1991; Mazza and Bertini, 2003). As observed for the majority of mammalian taxa (Clauss et al. 2013), Bergmann's rule should apply on a temporal scale. Therefore, it could be predicted that within the same species larger body sizes should evolve during colder stages of the Quaternary as compared to warmer interglacial stages. Early work on carnivores, such as the red fox (*Vulpes vulpes*) and spotted hyena (*Crocuta crocuta*), provided strong evidence of size changes related to Quaternary climate (Davis, 1977, 1981; Klein, 1986; Klein and Scott, 1989). When species interaction is considered, the support for climate-related body size changes in both fossils and modern carnivores is more equivocal (Dayan et al., 1991; Meiri et al., 2004).

Within this context, the cave bear (*Ursus spelaeus*) is an interesting case in point. Kurtén (1955) revealed the potentially rapid response rate of cave bear size to Pleistocene climatic changes, but no further support to this hypothesis has been proposed so far. Intensive studies into cave bear tooth morphology and skull variation have revealed differential geographical variation (Baryshnikov, 1998, 2006; Baryshnikov and Puzachenko, 2011; Goubel et al., 2012; Torres et al., 2002) with unclear patterns of temporal variation within the same population. Ursid dentition has been demonstrated to show dietary proclivity and adaptations to environments, giving insights into environmental stressors during certain temporal intervals in a population (Christiansen, 2007; Mattson, 1998; Sacco and Van Valkenburgh, 2004). Nevertheless, many other factors can impact morphological variation. The cave bear is a largely polymorphic species, with many sub-species being described in previous studies, and continuing arguments whether these variants represent separate species or sub-species status (Baryshnikov and Puzachenko, 2011; Grandal-d'Anglade and López-González, 2005; Grandal-d'Anglade and Vidal Romaní, 1997; Hofreiter et al., 2004; Rabeder et al., 2004). Spatial morphological differences in dentition have been found in cave bears throughout karstic networks (Rabeder et al., 2004, 2008), suggesting geographic isolation and lack of migration in the species as a likely culprit (Grandal-dAnglade and López González, 2004).

Rabeder (1983, 1999) and Baryshnikov (1998) demonstrated that cheek teeth analysed chronostratigraphically can acceptably detail a model of dental evolution. Seetah et al. (2012) investigated temporal variation in cave bears from different stratigraphic layers of Vindija cave in Croatia, finding no significant morphological variation across the thirty-thousand-year period analysed. This trend was argued to be the result of the highly flexible paleoecology of the cave bear whose herbivorous dietary habit has been a substantial matter of debate (Pacher and Stuart, 2009). A recent revision from Bocherens (2018) on cave bear palaeodiet, support strong overlap in $\delta^{15}N$ and $\delta^{13}C$ values between cave bears and large mammalian herbivores of the same temporal frame, although evidence of extreme herbivory in skull morphology is still controversial (Meloro, 2011; van Heteren et al. 2015, 2016).

Here, we investigate size and shape variation in a large sample of upper molars belonging to cave bears from Scladina Cave. Scladina Cave (Belgium) (Fig. 1) is of great importance in the field of Quaternary fauna, having unveiled Neanderthal remains in the complex of Units 4A and *U. spelaeus* assemblages throughout its complex chronostratigraphic sequence.

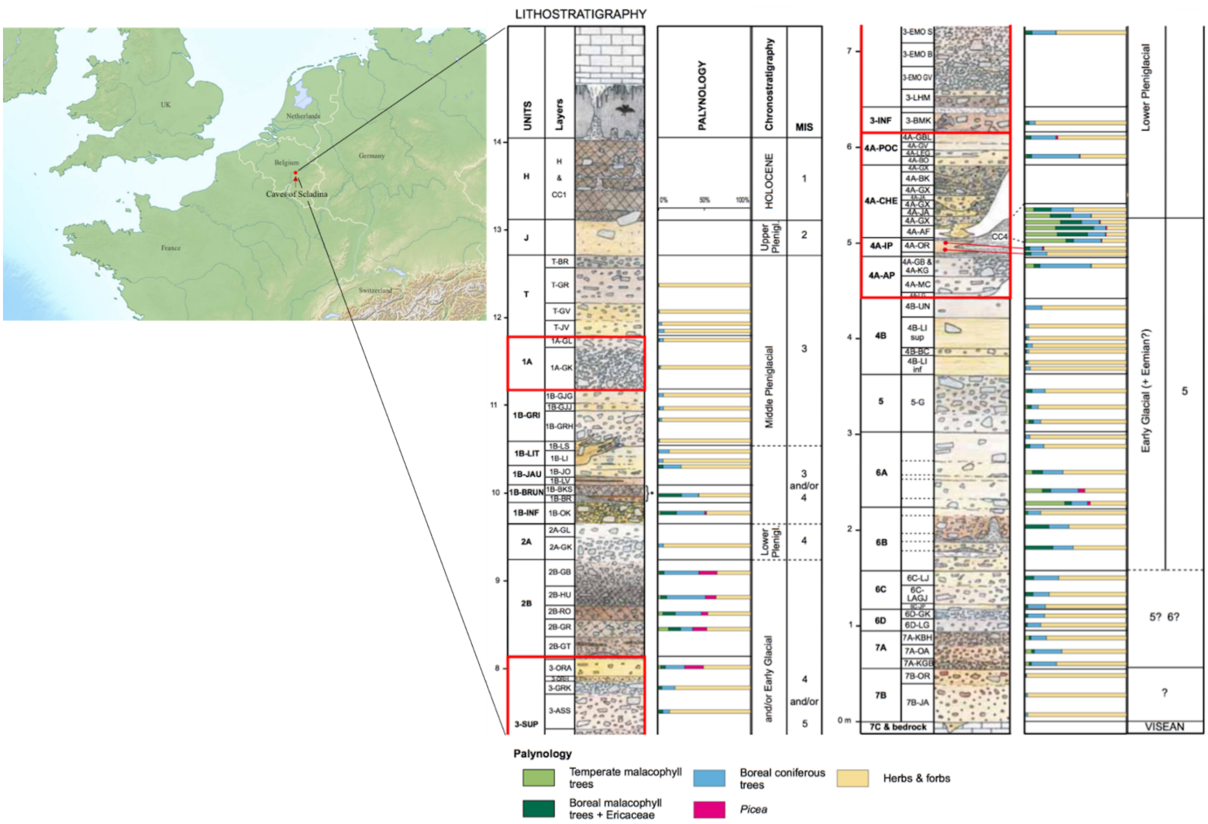

Fig. 1. A map of North-West Europe showing the position of Scladina Cave with its chronostratigraphic sedimentary sequence, including correlating marine oxygen isotope stages, palynology and chronostratigraphic time frames. Units analysed in this study are highlighted in red boxes (modified after Pirson et al., 2014).

Belgium continues to be a region of importance in the field of palaeontology, palaeoecology and palaeoanthropology, with research focusing on hominin and megafauna interaction (Abrams et al., 2014), anthropogenic and environmental impacts on *Ursus* species (Naito et al. 2016), cave bear life (Germonpré, 2004; Germonpré and Sablin, 2001), diet (Bocherens, 2009 and 2018; Peigné et al., 2009) and their skeletal morphology (Baryshnikov et al., 2003; Goubel et al., 2012). Despite such intense research focus, a chronostratigraphical analysis of the *U. spelaeus* assemblage is lacking for Scladina Cave.

By employing the geometric morphometric method (GMM, Adams et al., 2004, 2013) we aim to investigate temporal morphological variation in molar size and shape of cave bear from a geographically confined site. Both these aspects are expected to change over temporal scale in relation to climatic oscillations. Our sample spans c.ca 100,000 years, a period long enough for a large mammal to exhibit a degree of morphological change.

2. Materials and Methods

2.1 Sites and Specimens

All teeth used in this study are upper M^1 and M^2, derived from the stratigraphy of Scladina Cave (Sclayn, Belgium, Fig. 1). The village of Sclayn, Namur province, is situated on the border of high and middle Belgium, on a previous southern side tributary of the Meuse river, Ri de Pontaine. Scladina Cave, along with around 15 other smaller caves are set into the west wall of the Fond des Vaux valley (Dubois, 1981), with its porch 7m below a plateau. Sister caves Saint Paul and Sous Saint Paul interlink with this main cavity (5m south and 7m below, respectively), known as the "Caves of Sclayn" (50°29'8.034"N, 5°1'34.5684"E) (Bonjean et al., 2014; Pirson, 2007). Even though the network has been explored since the early 1950s, Scladina Cave was discovered by amateurs in 1971 and has been under scientific excavation since 1978 (Otte et al., 1983). The stratigraphy of Scladina expands over 15m in depth, comprising of 30+ units and 120+ layers (Pirson et al., 2008). Samples used here from Scladina Cave have been excavated over a 30-year period (1981-2001), under directors Marcel Otte (1978-1991) and Dominique Bonjean (1991-present). The teeth analysed have been exhumed from three major stratigraphic units, covering approximately 100,000 years: 1A (~38-40 kya; MIS 3), 3 (MIS 4 and/or 5) and 4A (< 153±15kya; MIS 5) (Pirson et al., 2014). Assemblage dates are based on other associated finds from corresponding strata using: radiometric dates on animal bone and dentition, on speleothem (Abrams et al., 2010; Bonjean et al*.,* 2011; Pirson et al., 2008), infrared stimulated luminescence on sediment (Unit 4B; Pirson et al., 2014), , gamma spectrometry on the Neanderthal mandible (complex of Units 4A) (Toussaint et al., 1998) and the general chronostratigraphic interpretation of the deposits (Pirson et al., 2014).

2.2 Landmark Configuration

All specimens investigated were first and second permanent upper molars (M^1 and M^2) housed in the Scladina site collection facility (for full list and catalogue number see Appendix). Right and left sided dentition were equally represented by n=169 and n=162.

The specimens were measured using an electronic calliper at 0.05 mm of accuracy and occlusal surface photographs taken if they met the exclusion criteria. Samples without complete linear measurements, worn to a point were placing landmarks became difficult, fractured distorting true size or fractured were a complete outline of the occlusal surface became unobtainable were excluded. These exclusion criteria resulted in 331 samples for geometric morphometric analysis.

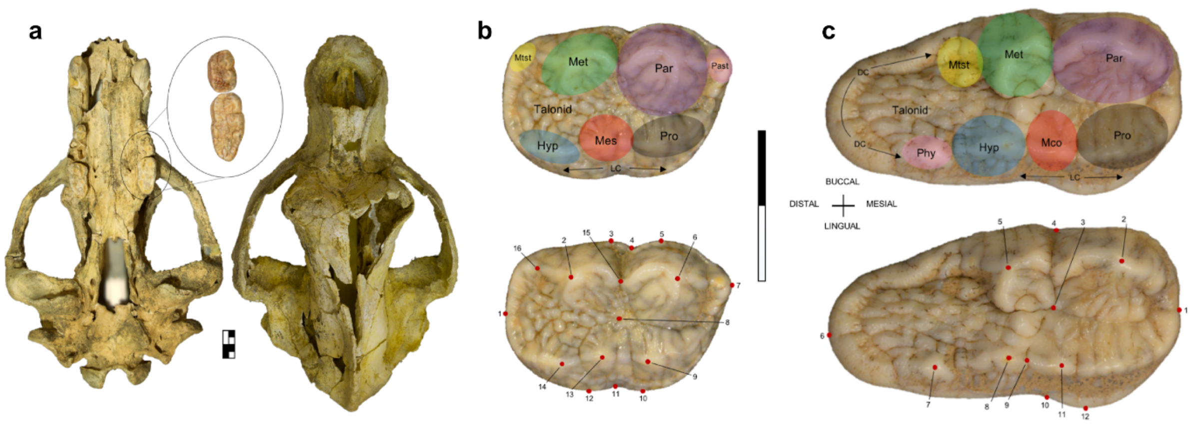

Fig. 2. (a) Inferior (left) and superior (right) view of *U. spelaeus* cranium, with focus to the M^1 and M^2. No SC-99-47-1 from stratigraphic units 4A of Scladina Cave. (**b**) (Above) Anatomical nomenclature for right upper M^1. (Below) Landmark configuration for right upper M^1. (**c**) (Above) Anatomical nomenclature for right upper M^2. (Below) Landmark configuration for right upper M^2. Refer to Table 1. for Description and methodology. Abbreviations are: Par = paracone, Met = metacone, Mtst = metastyle, Mes = mesocone (2nd (distal) protocone), Pro = protocone, Mco = metaconule (mesocone), Hyp = hypocone, Phy = post-hypocone, Past = parastyle, LC = lingual cingulum, DC = distal cingulum.

	Landmark	Definition
M^1	1	Central crease of Distal cingulum following the mesial/distal crease
	2	Peak of metacone
	3	Buccal apex of distal half
	4	Buccal crease between paracone and metacone
	5	Buccal apex of mesial half
	6	Peak of mesial paracone
	7	Peak of parastyle
	8	Internal valley of mesocone, paracone and metacone
	9	Peak of protocone

	10	Lingual apex of mesial half
	11	Lingual crease, lingual to the mesocone
	12	Lingual apex of distal half
	13	Peak of mesocone
	14	Peak of hypocone
	15	Valley between paracone and metacone, where the paracone and metacone curvilinear ridges meet
	16	Valley between metacone and metastyle, following curvilinear ridge
M^2		
	1	Central crease of mesial border following the mesial/distal crease
	2	Peak of paracone
	3	Internal valley of Distal (2nd) protocone (metaconule), paracone and metacone
	4	Buccal crease between paracone and metacone
	5	Peak of metacone
	6	Central crease of Distal cingulum following the mesial/distal crease
	7	Peak of distal cusp of hypocone (Peak of post-hypocone)
	8	Peak of mesial cusp of hypocone (peak of hypocone)
	9	Valley between hypocone and Distal (2nd) protocone (metaconule)
	10	Crease where cingulum meets crown lingually
	11	Peak of Distal (2nd) protocone (metaconule)
	12	Apex of cingulum

Table 1. Adapted definition and numbering sequence of landmarks for M^1 and M^2 (Rabeder 1999; Torres 1988; Tsoukala and Grandal-d'Anglade 2002; Von Den Driesch 1976).

Occlusal surface images of the dentition were taken using a Nikon D5300 and Sigma 105mm f2.8 OS EX DG Macro Lens at a general distance of 50 cm. Two-dimensional anatomical landmark coordinates were taken using the software tpsDIG2 (Rohlf, 2015). M^1 specimens were ultimately represented by 198 specimens covered by 16 landmarks while for the M^2 133 specimens were recorded with 12 landmarks (Fig. 2). The landmarks were chosen to cover the external tooth surface and the main / most visible cups. A full definition of the landmark configuration is shown in Table 1. All images, measurements and landmarks were taken by Daniel Charters only to alleviate inter-observer error.

2.3 Geometric Morphometrics (GMM)

Landmark configurations were superimposed separately for M^1 and M^2 using a Generalised Procrustes analysis (GPA). This procedure performs a rotation, translation and scaling of the original 2D Cartesian coordinates (Rohlf and Slice, 1990) in order to obtain a new set of coordinates named "Procrustes coordinates" that allow multivariate quantification of the shape for each specimen. Each landmark configuration was scaled to a unit centroid size (CS, this is defined as the centre of gravity of each configuration, produced by calculating the square root of the sum of squared distances from each landmark to the barycentre). Together with tooth length, CS (log transformed to ensure normality) was used as a proxy for specimen size.

In order to identify potential differences in tooth size and shape, each specimen was categorised according to its chronostratigraphic context (=layer). Size differences between specimens from different stratigraphic layers were tested using standard one-way analysis of variance (ANOVA) in SPSS (version 23.0) followed by post-hoc tests and visualised using box plots. Variation in tooth shape was tested adopting the Procrustes ANOVA test in the R package Geomorph (Adams and Collyer, 2015; Adams and Otarola-Castillo, 2013) with further pairwise permutation tests on both M^1 and M^2 shape coordinates. Visualisation and interpretation of the shape variation was conducted using Principal Component Analysis of shape coordinates in PAST (version 2.17, Hammer et al., 2001). PCA allows extrapolation of orthogonal vectors that describe major variation within a multivariate sample. Additionally, thin plate spline provides a way to show how shape changes occur along each PC vector relative to the mean (a configuration that is plotted at the origin of PC axis and shows no deformation).

In addition to standard PCA we also performed a between-group PCA (Mitteroecker and Bookstein, 2011) assuming layers as groups to characterise distinct tooth populations. The between-group PCA is rotational invariant and provides a different perspective on visualising specimen variation that is projected around group means. PCA and between group PCA scatter plots with 95% confidence ellipses and wireframe deformation grids were performed using PAST (version 2.17, Hammer et al., 2001).

Allometry was tested in MorphoJ (version 1.06) using log transformed CS as independent variable and Procrustes coordinates as dependent. This was repeated separately for each tooth and each layer to better identify if allometric variation explained different percentage of shape variance through time. Morphological disparity tests were also computed on shape PC scores to quantify variation in the multivariate shape space through time (Foote, 1992). By using the R package Geomorph morphological disparity was quantified for each layer and a permutation test was implemented to test for variance differences between layers. As sex could not be determined from the fossil samples, we were unable to perform any robust statistical assessment of sexual dimorphism. By checking size distribution for each layer there was no clear evidence of bi-modality and this did not allow us to determine subpopulations of small (eventually females) vs big (males) specimens within each layer.

3. Results

3.1 Tooth Size

ANOVAs for M^1 showed significant differences in length (=l) and width (=w) between stratigraphic layers (l: $F_{2, 195} = 9.197$, $P < 0.001$; w: $F_{2, 195} = 16.228$, $P < 0.001$. Post-hoc comparisons revealed specimens from units 3 to be significantly bigger in both length and width than the other units (1A $P < 0.01$, 4A $P < 0.001$) (Table 2). The Unit 1A and units 4A specimens were no different from each other.

Layer/Sample	1A	3	4A
1A	-	**0.003**	0.894
3	**0.0001**	-	**0.0001**
4A	0.896	**0.0001**	-

Table 2. *P* values expressed from Tukey HSD pairwise comparison test for M^1 length and width respectively, above and below the main diagonal. Significance is highlighted in bold.

M^2 length ($F_{2, 130} = 10.084$, $P < 0.001$) and width ($F_{2, 130} = 10.017$, $P < 0.001$) ANOVAs were equally significant. Second molars from units 4A (l: 43.6303 ± 3.07871, w: 22.3727 ± 1.30678) were smaller than Unit 1A (l: 46.2483 ± 2.41343, w: 23.5897 ± 1.32952, $P < 0.001$) and units 3 (l: 45.4824 ± 2.70567, w: 23.2505 ± 1.08956, $P < 0.05$) (Table 3).

M^1 and M^2 ANOVAs for log centroid size were equally significant ($P < 0.001$) (Fig. 3). Post-hoc tests showed that teeth from units 4A were significantly different from Unit 1A and units 3 in both M^1 and M^2 ($P < 0.001$ in all comparisons). Specimens from units 1A and 3 were not different in centroid size.

Layer/Sample	1A	3	4A
1A	-	0.339	**<0.001**
3	0.378	-	**0.010**
4A	**<0.001**	**0.009**	-

Table 3. P values expressed from Tukey HSD pairwise comparison test for M^2 length and width respectively, above and below the main diagonal. Significance is highlighted in bold.

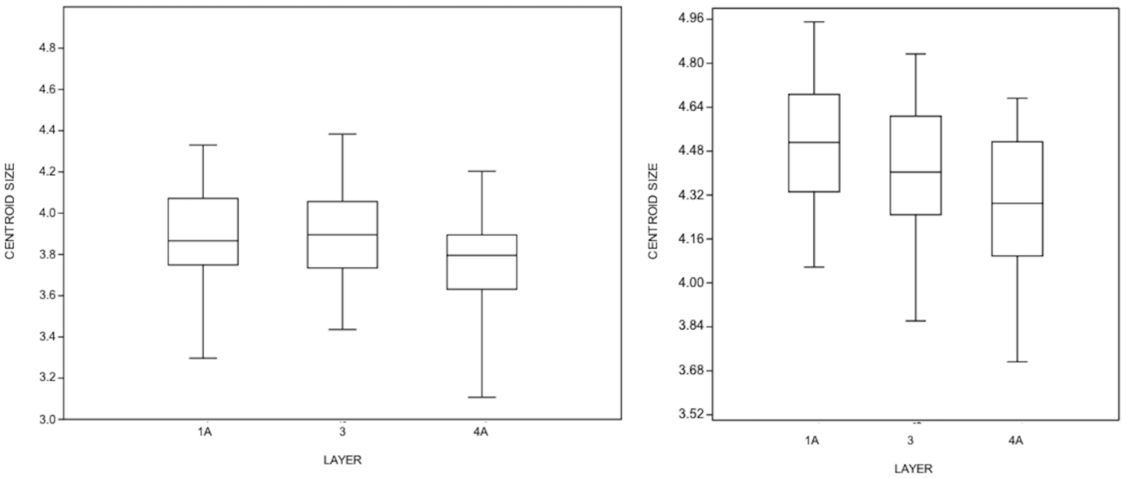

Fig. 3. (a) M^1 and (b) M^2 box plots of M^1 log centroid size showing means and quartile distribution.

3.2 Tooth shape

Procrustes ANOVA (Fig 4a and b.) for M^1 shape data showed significant differences between layers ($F = 8.9128$, $Z = 7.4593$, $df = 2, 195$, $P < 0.001$; $r^2 = 0.083757$). However, large overlap between groups was expressed visually in both standard and between group PCA scatter plots (standard = PC1 20.06%, PC2 12.429% var, between-group = PC1 86.411% var, PC2 13.589% var). Pairwise permutation tests were equally significant in all comparisons ($P < 0.01$ in all cases). Positive PC1 scores (generally associated with specimens from units 3) show an overall lingual shortening of M^1 mesiodistally, represented by a contraction of landmarks 10, 11 and 12. Most Unit 1A specimens, in comparison to units 3, clusters more negatively on PC1. This relates to a contraction between the peak of the hypocone and lingual apex. Units 4A specimens strongly overlap with units 1A and 3.

PC2 vector describes shape change of the cusp position, with positive scores showing enlargement of the paracone and metacone along with buccolingual widening. At the extremities, an expansion from internal valley (landmark 8) occurs on negative PC2 scores and a contraction on positive PC2 (Fig. 4a). All layers congregate towards a more neutral

PC2 score, positioning around the origin. The between-group PCA (Fig. 4b) did not provide a better discrimination with layers still consistently overlapping between PC1 and PC2.

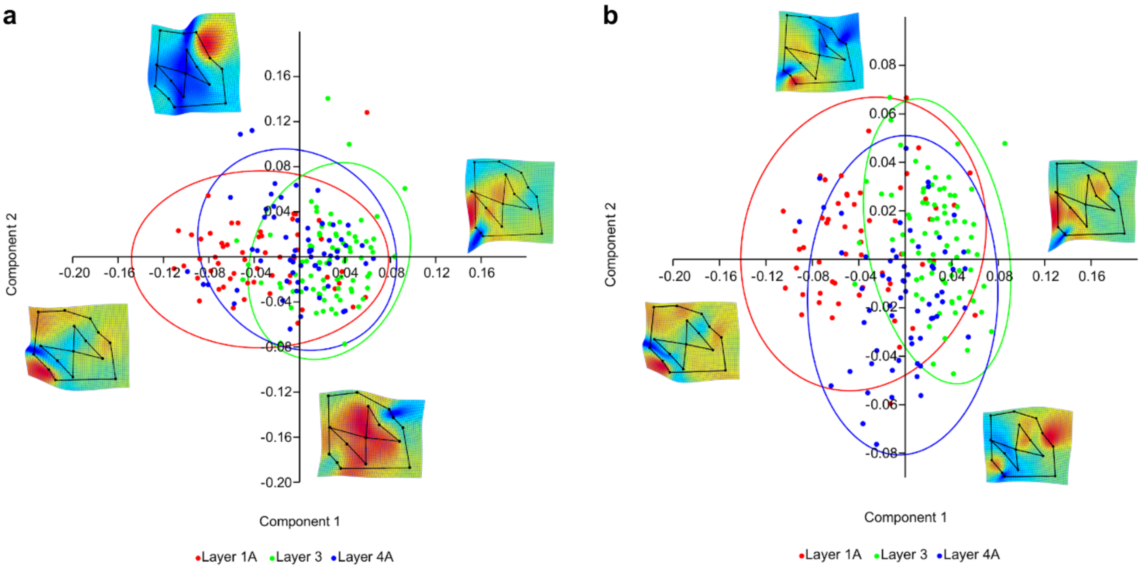

Fig. 4. (a) PCA scatter plot of M^1 with deformation grids and wireframes, PC1 20.06% var, PC2 12.429% var. PC1 0.1, -0.12, PC2 0.15, -0.08. (b) Between-group PCA scatter plot of M^1 with deformation grids and wireframes PC1 86.411% var, PC2 13.589% var. PC1 0.1, 0.12, PC2 0.08, -0.08. Temperature relating jacobian expansion factors are used to aid visualization (red shows expansion, blue shows contraction).

Procrustes ANOVA for M^2 shape equally resulted in statistically significant differences ($F = 2.6303$, $Z = 3.3477$, $df = 2, 130$, $P < 0.001$; $r^2 = 0.038892$). Pairwise permutation tests showed that all units 1A, 3 and 4A differ from each other in shape ($P < 0.01$ in all pairwise). The PCA scatter plot (PC1 18.862% var, PC2 14.832% var) still conveys a large overlap of layers analysed (Fig. 5a). In the between-group PCA scatter plot (Fig. 5b), shape difference was better presented. Specimens from Unit 1A score more positively on PC2, due to an expansion between the post-hypocone and hypocone, along with a more mesial positioning of the distal protocone. This contrasts with units 3 specimens that situate around the origin and negative PC2. Units 4A specimens are equally distinct in lingual cusp position and cingulum width (Fig. 5b).

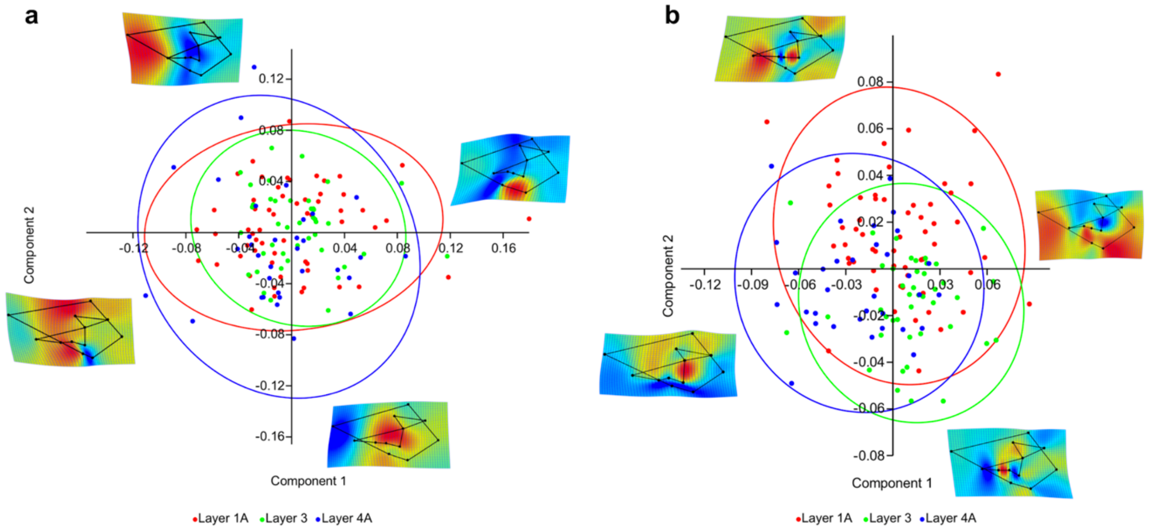

Fig. 5. (a) PCA of M^2 with deformation grids and wireframes, PC1 18.862% var, PC2 14.832% var. PC1 0.18, -0.12, PC2 0.13, -0.08. (b) Between-group PCA of M^2 with deformation grids and wireframes, PC1 57.483% var, PC2 42.517% var. PC1 0.09, -0.09 PC2 0.09, -0.06. Temperature relating jacobian expansion factors are used to aid visualization (red shows expansion, blue shows contraction).

3.3 Allometry and Disparity

Log centroid size had a small but significant impact on M^1 shape (R^2 = 0.011043, P < 0.02), but not on M^2 (R^2 = 0.012731, P = 0.0686). However, within the M^1 subsample of layers, only 4A exhibited significant allometric pattern (R^2 =0.048427, P < 0.001), with size increasing its percentage of variance explained on shape (from 1.1% of total sample to 4.84%). Even though allometric effect was not relevant in the M^2 total sample, units 4A specimens again showed centroid size to explain a significant proportion of shape variation (var. 6.900%, P < 0.02).

In both datasets, molars from units 4A displayed higher shape disparity compared to the other layers (Fig. 6). Pairwise comparisons showed units 4A disparity to be statistically significant from units 3 (M^1 P < 0.016, M^2 P < 0.027) that exhibited the lowest values (M^1 = 0.0074, M^2 = 0.0061) in both tooth types.

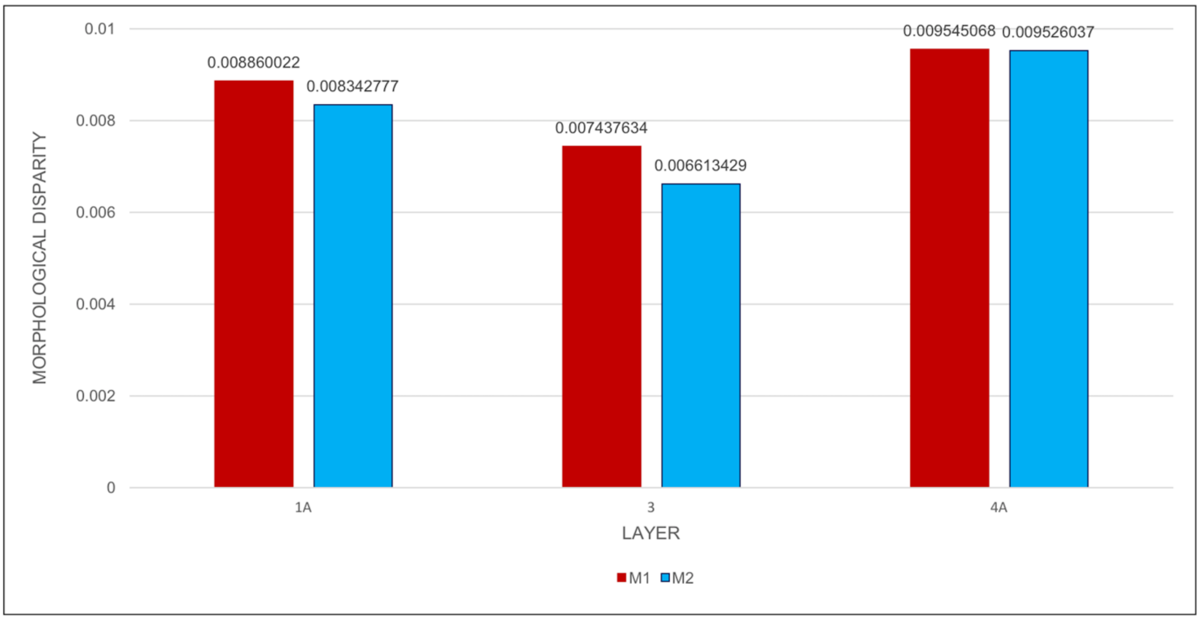

Fig. 6. Morphological disparity for M1 and M2 as shape variance for each stratigraphic units.

4. Discussion

This study shows that geometric morphometric offers an effective approach to investigate temporal morphological variation from a single site. Previously, morphology has been analysed to understand and separate populations of geographically variant cave bears, regardless of site proximity (Seetah et al., 2012). This has further been interpreted to detect genetic variation, climatic and dietary adaptations (Hofreiter et al., 2004; Stiller et al., 2014).

For the Scladina cave bears, we identified size variation in both M^1 and M^2. M^1 showed fluctuation between stratigraphic periods with no clear trend, while M^2 showed a clear size increase through time. For both molars, there was a size increase from units 4A to units 3, then a size reduction in M^1 and increase in M^2 from units 3 to 1A. This morphological change in the molars could relate to the processing of food. Cave bear cheek teeth are functionally crucial for the processing of tough, fibrous plant matter (Rabeder et al., 2000). Baryshnikov et al. (2003) suggested that morphological differences observed in the M^2 and M_3 are interpreted as adaptive, with bears occupying different environmental niches, or [as in this case] different climatic periods, showing differences in the size of their dentition.

Smaller dentition and reduced talonid section seen in PCA scatter plots for the complex of units 4A specimens could relate to a temperate climate with an abundance of more easily processed and varying food matter. The climatic improvement has been demonstrated for a part of this sedimentary complex where a thick stalagmite floor has been observed (Pirson et al., 2014). Indeed, a smaller tooth surface in bears is generally associated with the consumption and processing of softer food types. This is seen in dietary preferences of extant bears. Sacco and Van Valkenburgh (2004) suggested that morphological variation could separate dietary groups. They found that the molar grinding area is large and prominent in the herbivorous giant panda (due to prolonged mastication of hard bamboo), smaller in mixed diet omnivorous bears, third smallest in the hypercarnivorous polar bear (consuming soft flesh) and smallest in the insectivorous sloth bear that has little need for further processing of food. In an herbivorous species, as assumed for the cave bear, a smaller grinding platform that characterise specimens from units 4As could suggest lesser need for prolonged mastication of hard foods.

The pollen spectra of units 3 recorded a lower rate in trees than previous layers but they remain well represented by the genera *Pinus*, *Corylus, Juniperus* and *Betula* (Pirson, 2007, Pirson et al., 2008 and 2014). A size increase in both M^1 and M^2 in units 3 (MIS 5 and/or 4) compared to units 4A (MIS 5) could relate to climatic cooling. The change from a temperate forest environment to one more boreal will have resulted in a decrease of easily masticated plant material. Climatic cooling may be a pressing factor influencing adaptation in molariform dentition, to cope with the need to consume harder plant matter (Baryshnikov et al., 2003).

The clear dominance of herbs and forbs and low concentration of trees (<5%) for Unit 1A support an herbaceous steppe grassland environment (Fig. 1, Pirson et al., 2008, 2014). The presence of *Hippophae*, *Ephedra* and *Helianthemum*, additionally indicates an harsh open steppe environment. Different to the size increase from units 4A to 3, a decrease in M^1 size and increase in M^2 size from units 3 to 1A (MIS 3) was detected. The increase in M^2 may again be a resultant adaptation to the harder plant matter in the tundra environment supposed at that time. Bocherens et al. (1997) produced analysis of $\delta^{13}C$ and $\delta^{15}N$ isotope signatures of fossil mammal collagen from Unit 1A of Scladina Cave. They found that cave bears from Unit 1A had $\delta^{15}N$ signatures not significantly different from that of the strict herbivores at the same site while the brown bears from same unit showed values consistent with omnivory, as for extant brown bears. Contrasting this, $\delta^{15}N$ signatures have been found to be significantly affected by the physiology of dormancy in bears (Fernández-Mosquera et al., 2001), thus nitrogen-based inferences on bears diet could be equivocal.

Variation in trophic diversity is seen in extant ursids when faced with different environmental and climatic factors such as: snow, precipitation and temperature (Bojarska and Selva, 2012). These factors have been found to alter foraging behaviour, change in food habits and disturbed hibernation patterns (Berducou et al., 1983; Melis et al., 2010; Stringham, 1986), also seen in other omnivorous mammals (Bartoń and Zalewski, 2007; Melis et al., 2006; Zhou et al., 2011). For omnivorous bear species, the difficulty of foraging on mast (the fruit of forest trees, nuts, berries, acorns etc.) and plant material through harsh conditions proves less of a problem as their diet allows the consumption of animal protein, but for large, supposed strictly herbivorous bears such as *U. spelaeus* (Bocherens et al., 1997, 2006; Ward and Kynaston, 1995), this possibly resulted in a strong selective pressure. Further climatic cooling and presence of a suggested open steppe environment, relating to the more recent Unit 1A, would see the depletion or near eradication of mast producing tree species and reliable food source for fat storage.

Rabeder and Tsoukala (1990) suggested that environmental factors have an impact on adaptation rate, most of which relates with the latter stages of the Quaternary. Unit 1A bears may have been pressured to rapidly adapt to the environmental shift from mixed temperate/boreal forest (associated with layer 3 specimens) to an open steppe (associated with layer 1A specimens) (Pirson et al. 2008).

Expansion in the talonid section of dentition (which relates to consumption of hard mast, van Heteren et al. 2014, 2016) is conveyed in PCA plots. M^2 from Unit 1A showed an expansion between the post-hypocone and hypocone, positioning the hypocone more mesially, allowing for a larger talonid section. This is further shown in M^1 from Unit 1A, with an expansion between the central crease of distal cingulum (landmark 1) and the hypocone and metacone (landmark 2 and 14, respectively). M^2 dentition representing units 4A demonstrates a large difference in lingual cusp position and cingulum width, compared to that of units 1A and 3. This shows an overall reduction of buccolingual size for units 4A bears. PCA plots presented here do not provide many insights into occlusal shape variation with large group overlapping, but significant difference is highlighted throughout the statistical analyses. This could be due to the highly conservative shape of teeth. Shape variance increases in units 4A when bears are relatively smaller than in units 1A and 3, possibly due to a relatively more temperate environment and broader range of food types. Warmer climates and more diverse plant material may result in smaller sized bears, with more diverse tooth shape, having to deal with a broader range of food types. This may also associate with Bergmanns rule, with the lesser need to retain body heat.

Relating to the palynology of units 4A mentioned above, specimens from this layer associate with a temperate forest environment (Pirson et al., 2008). The period estimated for units 4A also produces questions about variability. The large timeframe of units 4A contain a harsh glacial and successive interglacial period (Pirson et al., 2014). Higher morphological variability in this layer may result in dentition adapting to two separate climatic environments. Uranium-Thorium ($^{234}U/^{230}Th$), gamma spectrometry, thermoluminescence and infrared stimulated luminescence dates spanning from~70-153kya (Pirson et al., 2014) contain both climatic events. Nevertheless, units 4A has been suggested of being a more temperate environment from ~120kya (Pirson et al., 2008), supported by size and shape differences found herein.

The lack of major morphological differences could also relate to population genetics, as this single site will show genetic constraint. Genetic exchange has been found to take place between bear populations in close geographic proximity, lowering morphological diversity (Baryshnikov, 2006; Baryshnikov et al., 2003; Rabeder, 1995; Rabeder et al., 2004, 2008; Stiller et al., 2013). Moreover, this supports research suggesting a genetic bottleneck in cave bears for an extended period before their extinction (Stiller et al., 2010).

4. Conclusion

Our research suggest that temporal morphological variation of cave bears can be shown statistically also over short temporal intervals. We identified changes especially in the talonid masticatory platform of M^2 dentition, whose expansion indicates adaptation towards a cool climatic cycle detected for the most recent Unit 1A. Reduction in the size of M^1 is also shown for this unit, suggesting maintenance of biomechanical performance of dentition for effective mastication as M^2 size increased. This morphological variation supoorts a rapid response to climatic factors pressuring consumable food sources, which for a proposed diet inflexible herbivorous species, would prove inimical.

Conflict of interest

There are no conflicts of interest.

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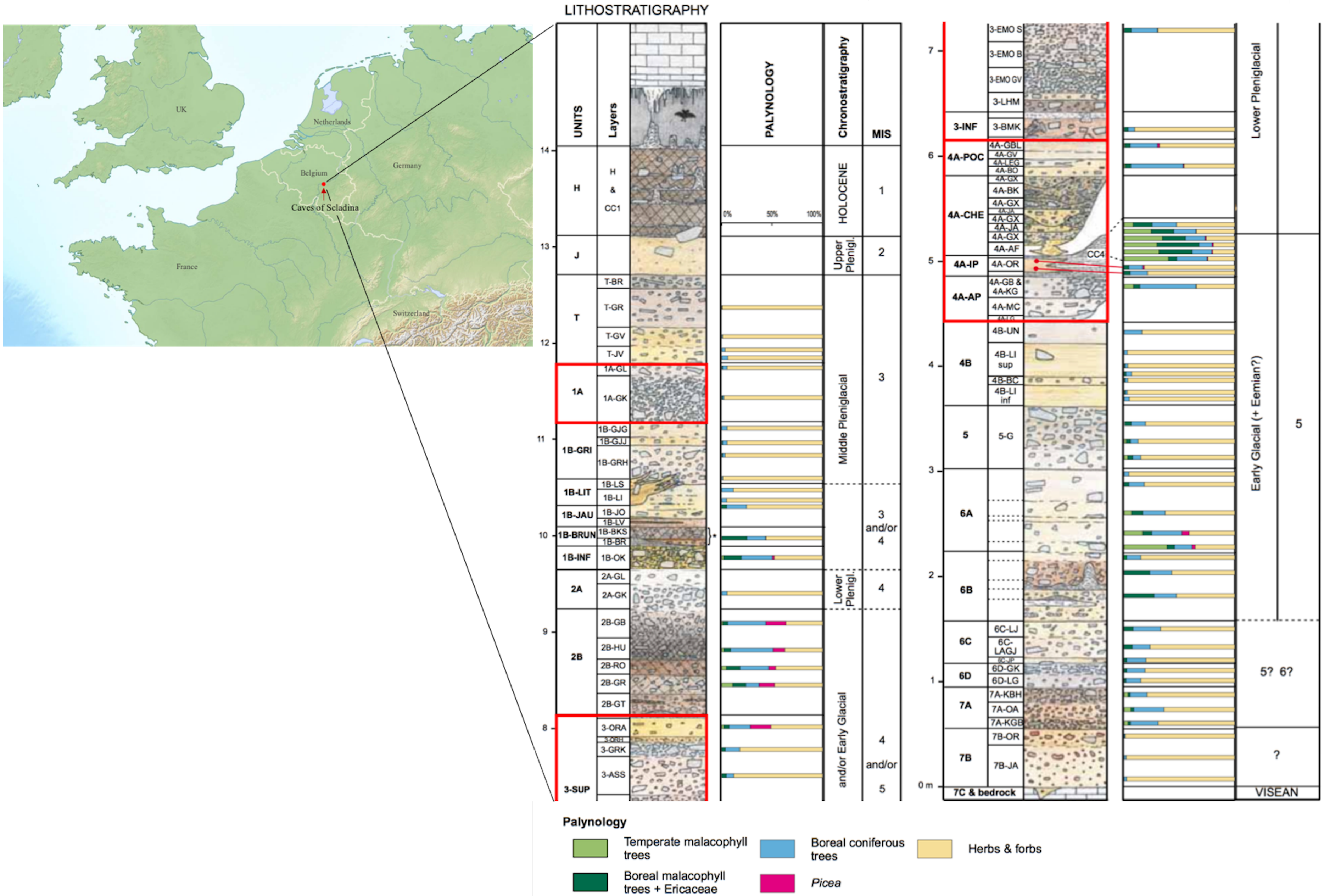
- Dentition of cave bears from Scladina cave shows morphological variation chronologically over time.
- Cave bear second upper molar became bigger over a short time period (from 153 to 40 kya) in relation to climatic cooling
- Shape changes in the upper molars are indicative of an increase in consumption of herbs and forbs for the Scladina cave bear during the latest 40 kya
- Tooth size and shape is a powerful ecomorphological predictors of cave bear dietary and climatic adaptations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3-EMO GV
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3-INF
3-BMK
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4A-LEG
4A-BO
4A-GX
4A-CHE
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4A-AP
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VISEAN
Palynology
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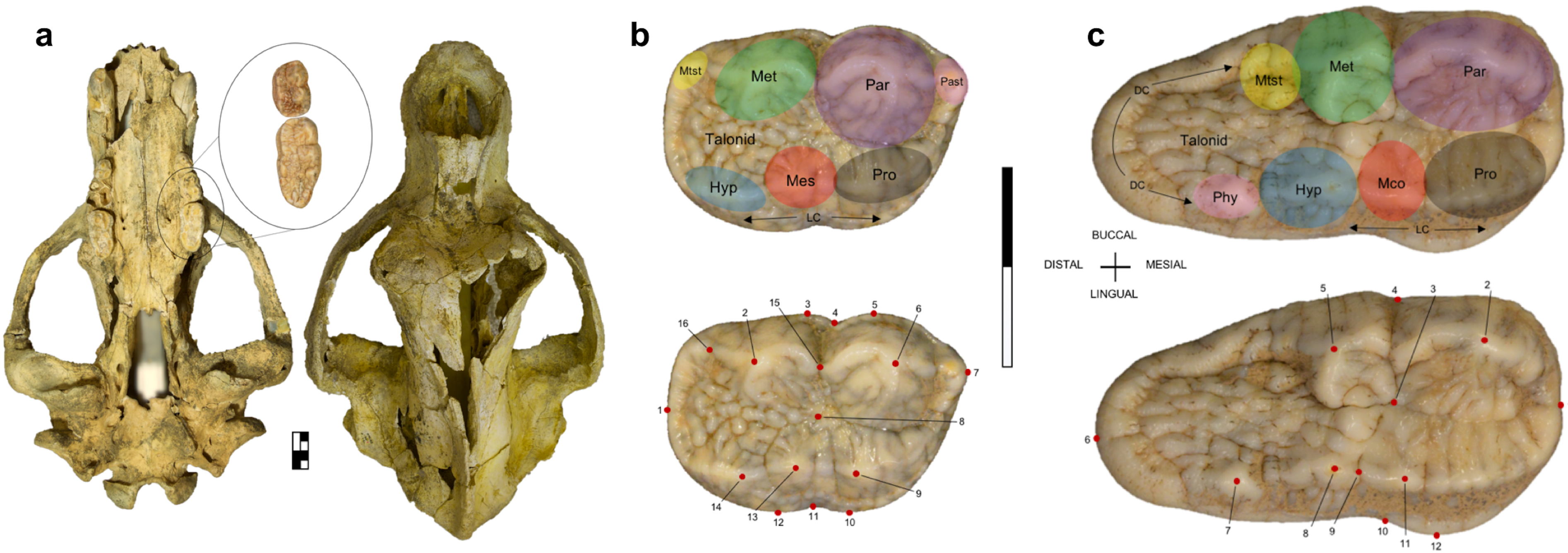
Boreal malacophyll trees + Ericaceae
Boreal coniferous trees
Picea
Herbs & forbs



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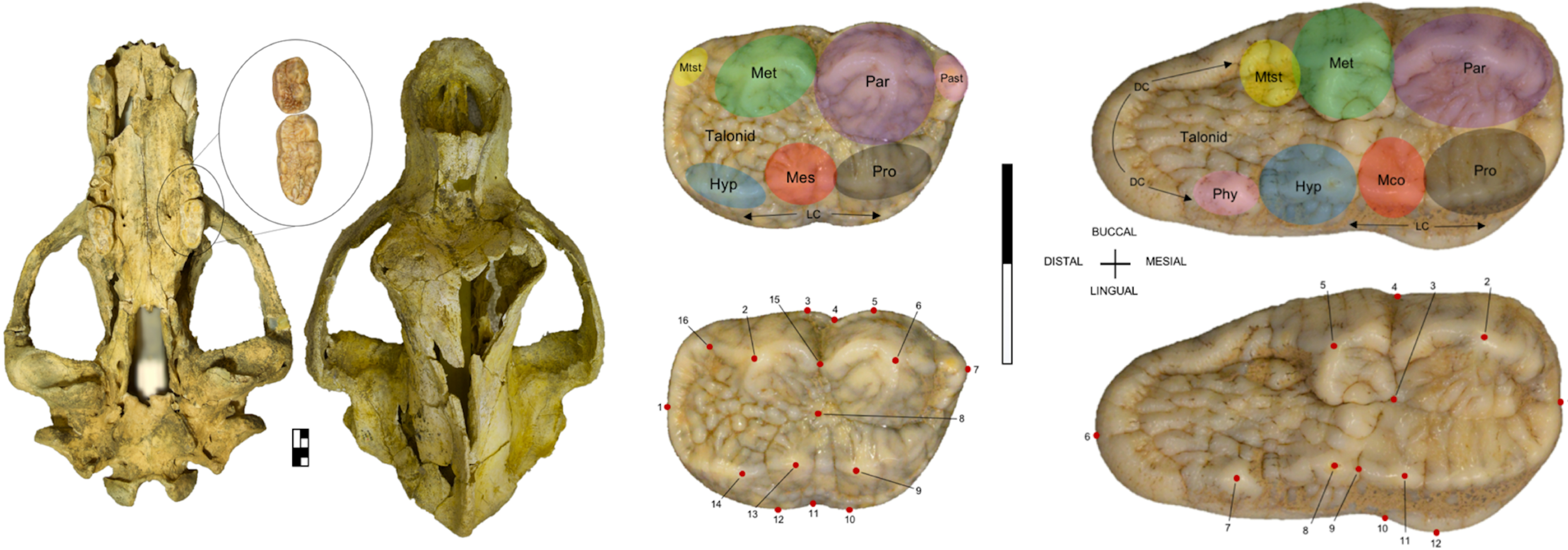

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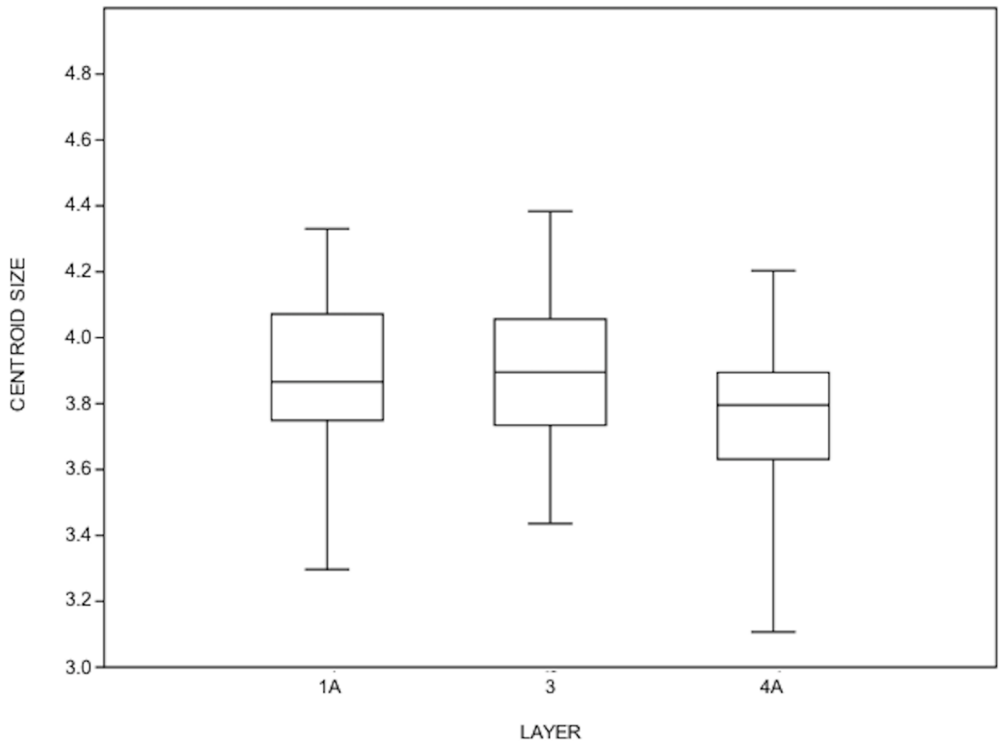
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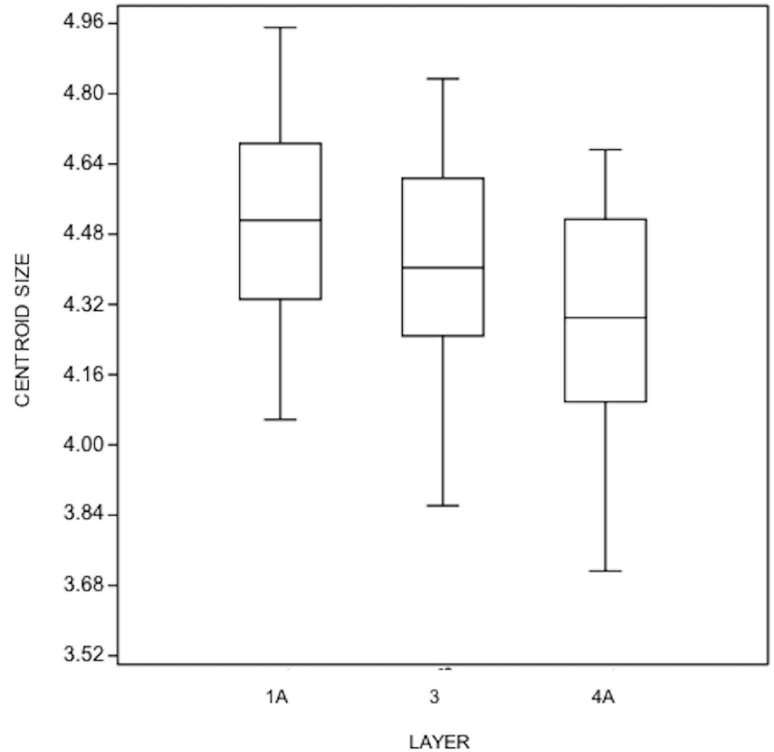
3
4A
LAYER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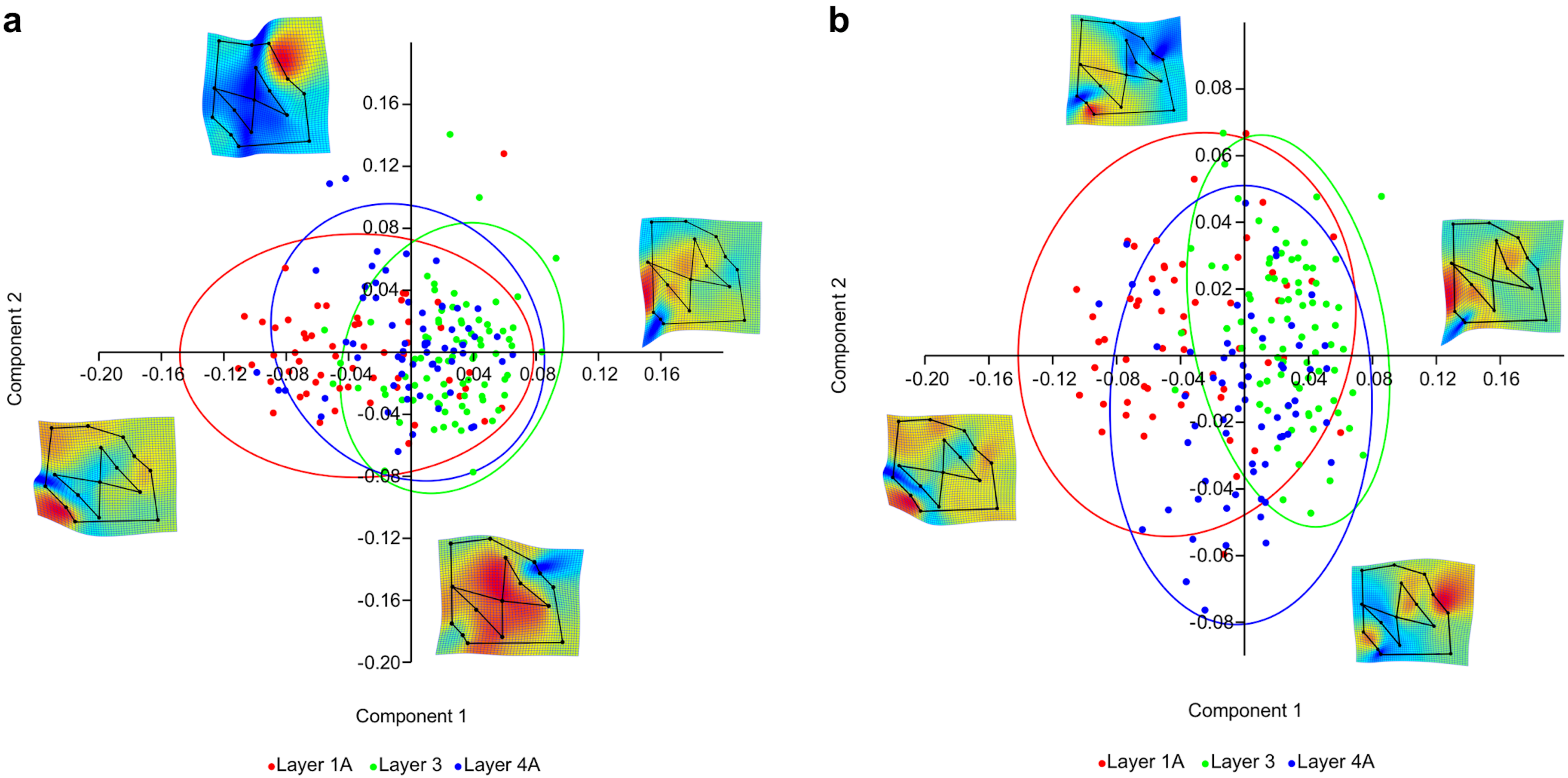
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b
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Component 2
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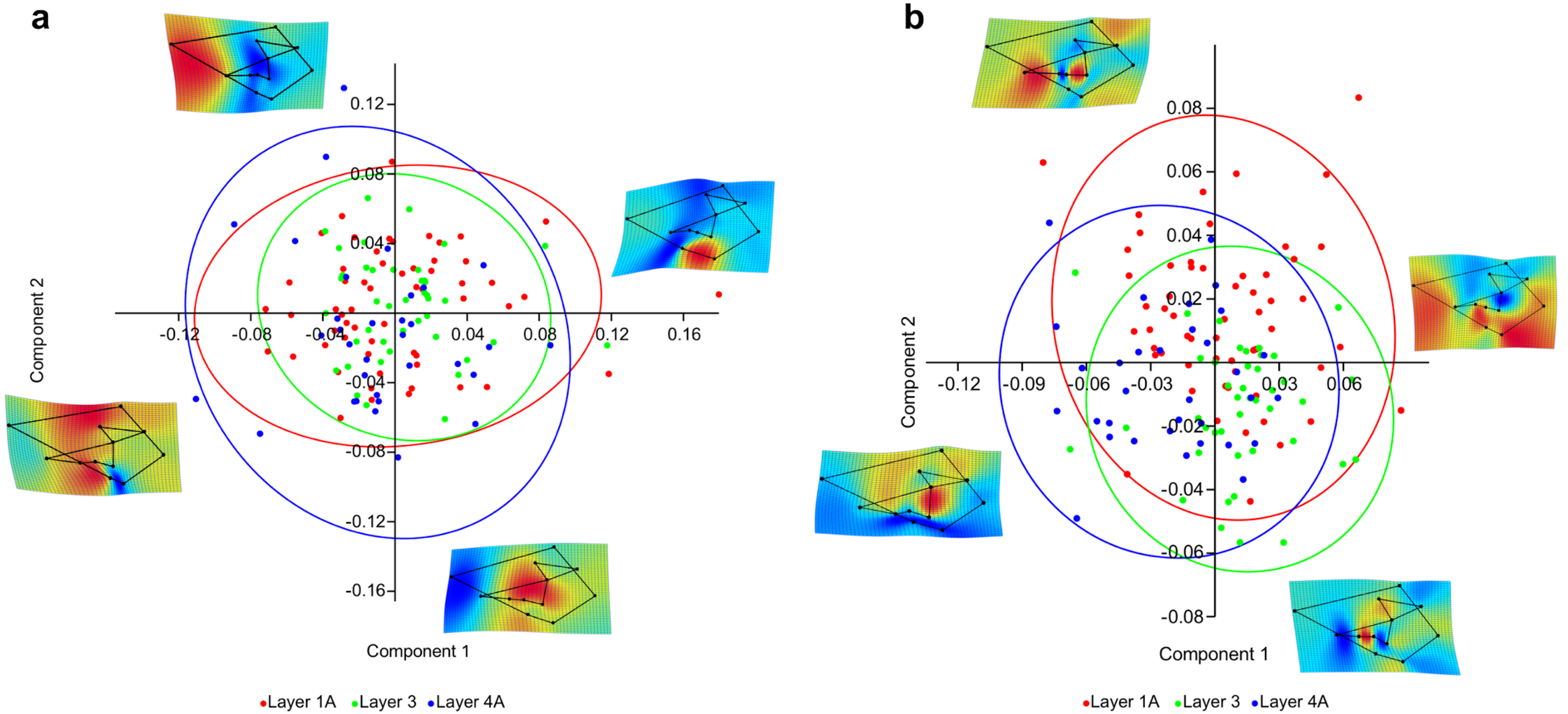
Layer 1A
Layer 3
Layer 4A



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0.12
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Layer 1A
Layer 3
Layer 4A
b
Component 2
Component 1
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0.06
0.04
0.02
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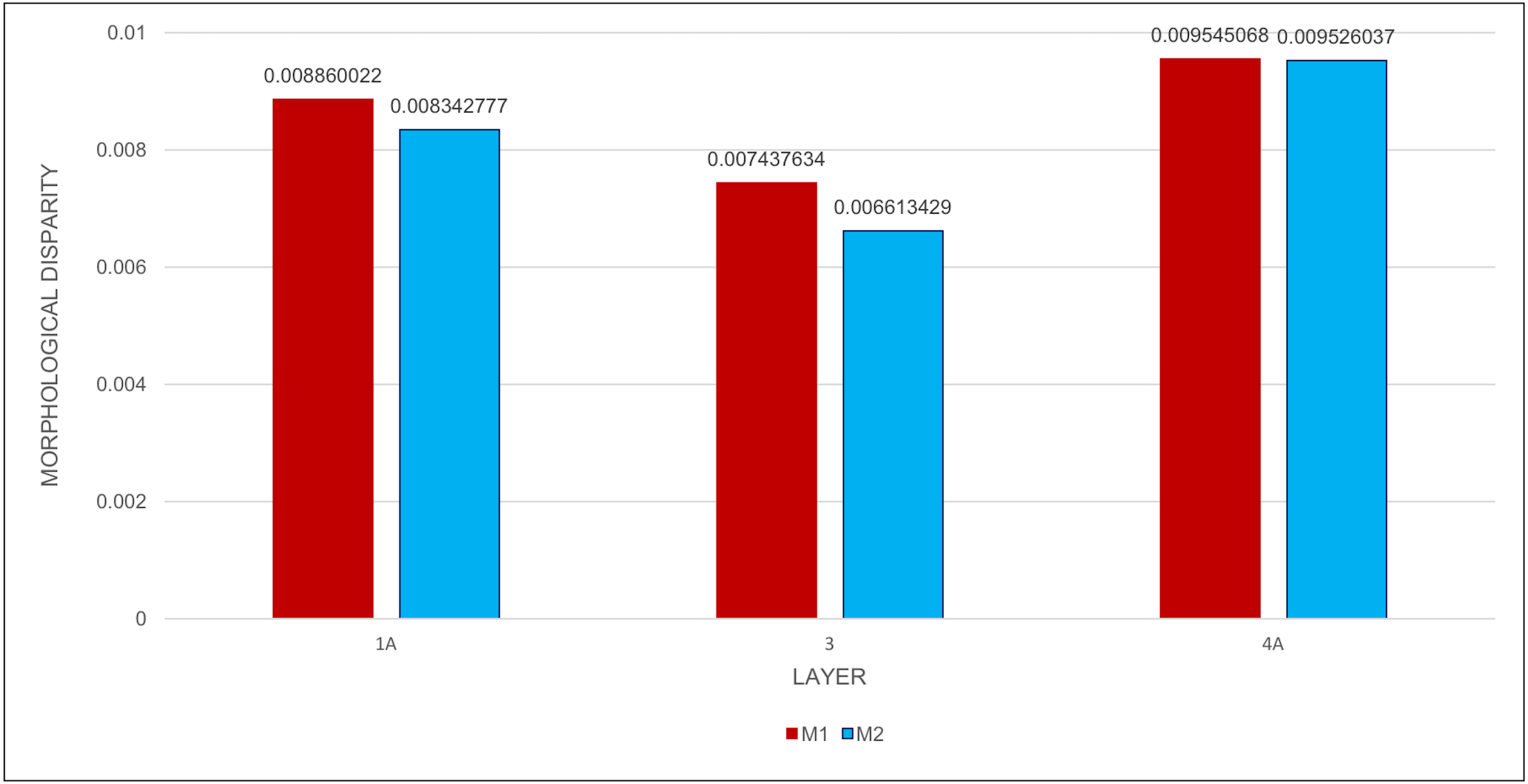
Layer 1A
Layer 3
Layer 4A



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4A
LAYER
M1
M2

Supplementary Material

Table. List of Cave Bear maxillary dentition used in Geometric Morphometric (GMM) analysis.

Invent number	Layer	Tooth	Length	Width	Ratio	Side	Species
SC 88 2-0-4	3	M1	31.33	21.54	145.450325	L	*U. spelaeus*
SC 88 92-0-4	3	M1	30.3	21.07	143.8063598	R	*U. spelaeus*
SC 92 375-0-72	3	M1	31.28	22.18	141.0279531	R	*U. spelaeus*
SC 92 430-0-3	3	M1	30.15	21.97	137.2325899	L	*U. spelaeus*
SC 92 435-0-47	3	M1	29.74	21.17	140.4818139	L	*U. spelaeus*
SC 92 582-0-40	3	M1	31.34	23.05	135.9652928	R	*U. spelaeus*
SC 93 163-0-16	3	M1	26.49	18.22	145.3896817	R	*U. spelaeus*
SC 93 511-9-4	3	M1	27.08	19.14	141.4838036	R	*U. spelaeus*
SC 94 392-0-4	3	M1	28.36	20.09	141.1647586	L	*U. spelaeus*
SC 94 451-0-1	3	M1	29.91	21.17	141.284837	L	*U. spelaeus*
SC 94 495-3-5	3	M1	27.56	20.61	133.7214944	R	*U. spelaeus*
SC 94 65-0-5	3	M1	27.25	19.64	138.7474542	R	*U. spelaeus*
SC 94 71-0-15	3	M1	25.97	18.13	143.2432432	R	*U. spelaeus*
SC 95 26-27-19	3	M1	30.76	21.02	146.3368221	L	*U. spelaeus*
SC 98 211-430-2	3	M1	29.75	21.14	140.7284768	L	*U. spelaeus*
SC 98 288-0-3	3	M1	28.57	20.64	138.4205426	R	*U. spelaeus*
SC 88 2-0-3	3	M1	28.97	19.79	146.3870642	R	*U. spelaeus*
SC 91 590-0-4	3	M1	30.13	21.38	140.9260992	L	*U. spelaeus*
SC 92 398-0-6	3	M1	27.96	19.16	145.9290188	R	*U. spelaeus*
SC 92 428-0-14	3	M1	30.88	21.26	145.2492944	L	*U. spelaeus*
SC 92 434-0-11	3	M1	27.86	16.76	166.2291169	L	*U. spelaeus*
SC 92 434-0-22	3	M1	30.2	20.94	144.2215855	L	*U. spelaeus*
SC 92 434-0-2	3	M1	31.52	22.54	139.8402839	R	*U. spelaeus*
SC 92 438-0-10	3	M1	29.07	20.57	141.322314	R	*U. spelaeus*
SC 92 438-0-26	3	M1	27.52	19.13	143.857815	R	*U. spelaeus*
SC 92 582-87-1	3	M1	27.07	19.16	141.2839248	L	*U. spelaeus*
SC 93 322-0-5	3	M1	27.59	19.45	141.8508997	L	*U. spelaeus*
SC 94 351 -0-5	3	M1	30.5	20.48	148.9257813	R	*U. spelaeus*
SC 94 495-3-16	3	M1	32.43	22.22	145.949595	R	*U. spelaeus*
SC 94 497-0-2	3	M1	31.4	20.48	153.3203125	R	*U. spelaeus*
SC 94 65-0-7	3	M1	30.82	21.46	143.6160298	L	*U. spelaeus*
SC 94 71-0-10	3	M1	29.25	20.36	143.6640472	R	*U. spelaeus*
SC 95 103-0-148	3	M1	29.36	21.21	138.4252711	R	*U. spelaeus*
SC 95 18-34-3	3	M1	28.23	20.17	139.9603371	L	*U. spelaeus*
SC 95 48-22-7	3	M1	29.58	20.57	143.8016529	R	*U. spelaeus*
SC 95 58-23-7	3	M1	27.28	19.91	137.0165746	L	*U. spelaeus*
SC 95 69-0-42	3	M1	26.25	17.47	150.2575844	R	*U. spelaeus*
SC 98 288-0-1	3	M1	31.35	20.56	152.4805447	L	*U. spelaeus*
SC 81 123-0-735	3	M1	27.67	19.55	141.5345269	R	*U. spelaeus*

SC 82 144-0-704	3	M1	30.39	21.61	140.6293383	L	*U. spelaeus*
SC 82 303-0-770	3	M1	29.14	20.13	144.7590661	L	*U. spelaeus*
SC 83 108-0-739	3	M1	28.02	18.58	150.8073197	L	*U. spelaeus*
SC 83 152-0-243	3	M1	28.58	19.62	145.667686	R	*U. spelaeus*
SC 83 267-0-757	3	M1	27.86	19.61	142.0703723	L	*U. spelaeus*
SC 83 269-0-689	3	M1	29.52	20.4	144.7058824	L	*U. spelaeus*
SC 85 121-0-741	3	M1	28.2	20.31	138.8478582	R	*U. spelaeus*
SC 85 153-0-736	3	M1	26.58	19.09	139.2352017	L	*U. spelaeus*
SC 85 159-0-707	3	M1	27.28	19.47	140.1129944	R	*U. spelaeus*
SC 85 173-0-703	3	M1	28.33	20.02	141.5084915	R	*U. spelaeus*
SC 86 139-2-752	3	M1	27.87	18.75	148.64	L	*U. spelaeus*
SC 86 144-0-751	3	M1	27.34	19.37	141.1461022	R	*U. spelaeus*
SC 87 140-0-705	3	M1	29.9	20.65	144.7941889	R	*U. spelaeus*
SC 87 162-0-742	3	M1	29.56	20.78	142.2521655	L	*U. spelaeus*
SC 87 23-0-75	3	M1	26.93	19.22	140.1144641	R	*U. spelaeus*
SC 87 32-0-74	3	M1	26.12	18.88	138.3474576	L	*U. spelaeus*
SC 87 84-0-695	3	M1	32.45	23.14	140.2333621	R	*U. spelaeus*
SC 88 27-0-722	3	M1	29.85	20.82	143.3717579	L	*U. spelaeus*
SC 90 43-0-761	3	M1	29.6	20.72	142.8571429	L	*U. spelaeus*
SC 91 297-0-4396	3	M1	28.1	19.36	145.1446281	L	*U. spelaeus*
SC 92 340-0-737	3	M1	27.98	19.49	143.5608004	R	*U. spelaeus*
SC 92 407-0-699	3	M1	28.95	21.01	137.7915278	L	*U. spelaeus*
SC 92 458-0-714	3	M1	26.54	18.21	145.7440967	L	*U. spelaeus*
SC 95 219-16-288	3	M1	29.41	20.19	145.6661714	R	*U. spelaeus*
SC 95 271 -0-717	3	M1	28.71	20.77	138.2282138	R	*U. spelaeus*
SC 95 495-0-686	3	M1	30.97	20.85	148.5371703	R	*U. spelaeus*
SC 95 53-0-698	3	M1	28.41	19.79	143.5573522	R	*U. spelaeus*
SC 99 182-309-772	3	M1	29.42	21.73	135.3888633	R	*U. spelaeus*
SC 01 132-0-5	3	M1	30.36	21.24	142.9378531	R	*U. spelaeus*
SC 01 21-18-0	3	M1	27.19	18.73	145.1681794	R	*U. spelaeus*
SC 01 94-0-0	3	M1	27.73	19.46	142.4974306	R	*U. spelaeus*
SC 81 126-0-734	3	M1	30.67	21.69	141.4015675	R	*U. spelaeus*
SC 81 44-0-685	3	M1	29.76	20.01	148.7256372	L	*U. spelaeus*
SC 82 254-0-753	3	M1	29.86	21.08	141.6508539	L	*U. spelaeus*
SC 85 143-0-740	3	M1	28.52	21.61	131.9759371	R	*U. spelaeus*
SC 85 158-0-768	3	M1	29.7	20.79	142.8571429	L	*U. spelaeus*
SC 87 31-0-689	3	M1	28.79	20.35	141.4742015	R	*U. spelaeus*
SC 89 31 -0-290	3	M1	27.33	19.17	142.5665102	L	*U. spelaeus*
SC 91 159-0-713	3	M1	30.48	20.66	147.5314618	L	*U. spelaeus*
SC 91 177-0-763	3	M1	28.63	20.31	140.9650419	R	*U. spelaeus*
SC 91 208-0-726	1A	M1	24.1	16.1	149.689441	R	*U. spelaeus*
SC 91 213-0-720	1A	M1	24.1	19.1	126.1780105	R	*U. spelaeus*
SC 91 286-0-697	1A	M1	24.1	17.4	138.5057471	R	*U. spelaeus*

SC 91 303-0-758	1A	M1	24.1	16.9	142.6035503	L	*U. spelaeus*
SC 91 379-0-694	1A	M1	24.1	18.4	130.9782609	R	*U. spelaeus*
SC 91 74-0-4170	1A	M1	24.1	18.3	131.6939891	R	*U. spelaeus*
SC 91 78-0-744	1A	M1	24.1	20.7	116.4251208	L	*U. spelaeus*
SC 92 111-0-721	1A	M1	27.6	18.6	148.3870968	R	*U. spelaeus*
SC 92 376-269-76	1A	M1	28.3	18.2	155.4945055	L	*U. spelaeus*
SC 92 397-286-732	1A	M1	29.6	19.9	148.7437186	L	*U. spelaeus*
SC 92 449-0-767	1A	M1	25.2	17.1	147.3684211	L	*U. spelaeus*
SC 94 397-0-723	1A	M1	28.5	18.7	152.4064171	L	*U. spelaeus*
SC 95 526-0-771	1A	M1	27.1	18.1	149.7237569	L	*U. spelaeus*
SC 95 531-0-887	1A	M1	26.4	17.6	150	L	*U. spelaeus*
SC 99 491-0-693	1A	M1	27.9	19.5	143.0769231	R	*U. spelaeus*
SC 91 558-0-2	1A	M1	27.4	18.7	146.5240642	L	*U. spelaeus*
SC 92 332-25-23	1A	M1	31.6	20.8	151.9230769	R	*U. spelaeus*
SC 92 332-25-3	1A	M1	29.9	19.6	152.5510204	L	*U. spelaeus*
SC 92 332-0-23	1A	M1	27.6	19.9	138.6934673	L	*U. spelaeus*
SC 92 429-0-7	1A	M1	29.2	19.7	148.2233503	L	*U. spelaeus*
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SC 95 468-0-83	1A	M1	27.8	18.9	147.0899471	L	*U. spelaeus*
SC 96 249-0-87	1A	M1	30.7	20.4	150.4901961	L	*U. spelaeus*
SC 97 37 -0-154*	1A	M1	28	19.2	145.8333333	L	*U. spelaeus*
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SC 92 422-0-2	1A	M1	31.2	20.7	150.7246377	L	*U. spelaeus*
SC 94 530-0-4	1A	M1	31.2	21.2	147.1698113	L	*U. spelaeus*
SC 95 283-0-227	1A	M1	29.1	19	153.1578947	R	*U. spelaeus*
SC 95 79-0-8	1A	M1	27.7	18.8	147.3404255	L	*U. spelaeus*
SC 95 82-0-28	1A	M1	30.4	21.2	143.3962264	R	*U. spelaeus*
SC 95 93-0-43	1A	M1	30.2	20.2	149.5049505	R	*U. spelaeus*
SC 96 210-46-1	1A	M1	27.8	18.8	147.8723404	R	*U. spelaeus*
SC 96 210-0-45	1A	M1	28.5	20.2	141.0891089	R	*U. spelaeus*
SC 98 171-0-91	1A	M1	26.8	18.7	143.315508	R	*U. spelaeus*
SC 99 73-0-96	1A	M1	29.1	19.4	150	L	*U. spelaeus*
SC 82 11-0-1	1A	M1	30.3	19.8	153.030303	R	*U. spelaeus*
SC 90 35-0-7	1A	M1	28.4	20	142	R	*U. spelaeus*
SC 91 425-0-2	1A	M1	30.9	22	140.4545455	R	*U. spelaeus*
SC 95 25-39-15	1A	M1	27.3	18.2	150	R	*U. spelaeus*
SC 95 25-39-20	1A	M1	26.3	18.4	142.9347826	R	*U. spelaeus*
SC 95 36-41-20	1A	M1	30.1	21.4	140.6542056	L	*U. spelaeus*
SC 86 59-0-3	1A	M1	28.4	18.7	151.8716578	R	*U. spelaeus*
SC 89 1 -0-1	1A	M1	30.2	20.6	146.6019417	R	*U. spelaeus*
SC 89 46-0-4	1A	M1	26.2	18.5	141.6216216	L	*U. spelaeus*
SC 90 172 -0-8	1A	M1	27.3	18.5	147.5675676	R	*U. spelaeus*

SC 91 425-0-3	1A	M1	28.5	21.1	135.07109	L	*U. spelaeus*
SC 91 461 -0-27	1A	M1	28.9	19.6	147.4489796	R	*U. spelaeus*
SC 91 527-0-4	1A	M1	29.8	20.3	146.7980296	L	*U. spelaeus*
SC 95 62-128-11	1A	M1	30.8	20.1	153.2338308	L	*U. spelaeus*
SC 91 537-0-3	1A	M1	26.2	17	154.1176471	L	*U. spelaeus*
SC 93 25-0-97	1A	M1	27	17.5	154.2857143	R	*U. spelaeus*
SC 93 325-49-13	1A	M1	28.4	19.5	145.6410256	L	*U. spelaeus*
SC 93 59-0-145	1A	M1	27.9	19.7	141.6243655	R	*U. spelaeus*
SC 91 598-0-3	1A	M1	27	19	142.1052632	L	*U. spelaeus*
SC 93 25-0-3	1A	M1	31.3	20.4	153.4313725	R	*U. spelaeus*
SC 00 131-814-57	4A	M1	28.9	19.2	150.5208333	R	*U. spelaeus*
SC 82 64-0-2203	4A	M1	26.6	18.8	141.4893617	L	*U. spelaeus*
SC 83 109-0-1968	4A	M1	26.7	18.3	145.9016393	R	*U. spelaeus*
SC 83 282-0-750	4A	M1	29.4	21.3	138.028169	L	*U. spelaeus*
SC 83 72-0-3170	4A	M1	24.4	18.9	129.1005291	L	*U. spelaeus*
SC 88 8-0-2200	4A	M1	28.5	18.5	154.0540541	L	*U. spelaeus*
SC 89 10-0-2201	4A	M1	28.6	19.2	148.9583333	R	*U. spelaeus*
SC 89 28-0-1925	4A	M1	27	18	150	L	*U. spelaeus*
SC 90 147-0-2198	4A	M1	24.9	16.2	153.7037037	R	*U. spelaeus*
SC 90 99-0-2196	4A	M1	27.7	18.6	148.9247312	L	*U. spelaeus*
SC 91 494-0-2	4A	M1	27.1	17.6	153.9772727	L	*U. spelaeus*
SC 91 502-0-2	4A	M1	25.3	18	140.5555556	L	*U. spelaeus*
SC 91 595-0-1	4A	M1	28.8	20.2	142.5742574	L	*U. spelaeus*
SC 91 597-0-4	4A	M1	28.4	19.9	142.7135678	R	*U. spelaeus*
SC 91 603-0-3	4A	M1	30.1	20.1	149.7512438	R	*U. spelaeus*
SC 91 613-0-10	4A	M1	29.8	20.7	143.9613527	R	*U. spelaeus*
SC 92 13-488-2	4A	M1	26.5	18.2	145.6043956	L	*U. spelaeus*
SC 92 18-0-2199	4A	M1	25.8	16.1	160.2484472	R	*U. spelaeus*
SC 92 36-0-3	4A	M1	26.2	17.9	146.3687151	L	*U. spelaeus*
SC 94 299-534-0	4A	M1	27.8	20.6	134.9514563	L	*U. spelaeus*
SC 94 3-195-0	4A	M1	29.2	20.2	144.5544554	L	*U. spelaeus*
SC 95 172-58-0	4A	M1	28.6	19.8	144.4444444	L	*U. spelaeus*
SC 95 181 -91-8	4A	M1	30.2	20.2	149.5049505	R	*U. spelaeus*
SC 95 186-411-0	4A	M1	28.9	21.1	136.9668246	L	*U. spelaeus*
SC 95 297-120-0	4A	M1	26.5	18.7	141.7112299	L	*U. spelaeus*
SC 95 387-164-0	4A	M1	28	20	140	R	*U. spelaeus*
SC 95 388-86-0	4A	M1	28.1	19	147.8947368	L	*U. spelaeus*
SC 95 71-458-0	4A	M1	29.1	20.5	141.9512195	L	*U. spelaeus*
SC 96 203-23-3172	4A	M1	28.5	19.2	148.4375	R	*U. spelaeus*
SC 97 10-106-0	4A	M1	28.3	19.4	145.8762887	L	*U. spelaeus*
SC 97 129-468-0	4A	M1	28.2	19.3	146.1139896	R	*U. spelaeus*
SC 97 73-365-0	4A	M1	28.5	19.9	143.2160804	R	*U. spelaeus*
SC 97 76-515-0	4A	M1	30	22.4	133.9285714	R	*U. spelaeus*

SC 98 286-272-0	4A	M1	26	17.9	145.2513966	R	*U. spelaeus*
SC 98 326-11-0	4A	M1	27.4	19.9	137.6884422	L	*U. spelaeus*
SC 00 109-186-0	4A	M1	26.2	18.7	140.1069519	L	*U. spelaeus*
SC 82 64-0-2202	4A	M1	28.2	20.1	140.2985075	R	*U. spelaeus*
SC 83 63-0-2197	4A	M1	30.2	19.9	151.758794	L	*U. spelaeus*
SC 86 104-0-1384	4A	M1	24.5	16.9	144.9704142	R	*U. spelaeus*
SC 90 81-0-10	4A	M1	24.9	16.7	149.1017964	L	*U. spelaeus*
SC 90 81-0-18	4A	M1	27.8	19.5	142.5641026	R	*U. spelaeus*
SC 90 81-0-15	4A	M1	25.9	18.3	141.5300546	R	*U. spelaeus*
SC 91 406-0-5	4A	M1	28.1	19.8	141.9191919	L	*U. spelaeus*
SC 91 620-0-8	4A	M1	29	20.9	138.7559809	R	*U. spelaeus*
SC 92 26-0-8	4A	M1	28	19.5	143.5897436	R	*U. spelaeus*
SC 92 6-0-15	4A	M1	29.5	20.2	146.039604	L	*U. spelaeus*
SC 92 6-0-16	4A	M1	30.6	22.1	138.4615385	R	*U. spelaeus*
SC 93 115-191-0	4A	M1	26.9	19.2	140.1041667	R	*U. spelaeus*
SC 94 246-467-0	4A	M1	27.7	20	138.5	L	*U. spelaeus*
SC 94 99-380-0	4A	M1	26.7	19.1	139.7905759	L	*U. spelaeus*
SC 95 177-80-0	4A	M1	26.7	17.5	152.5714286	R	*U. spelaeus*
SC 95 181 -92-4	4A	M1	28.9	20.2	143.0693069	L	*U. spelaeus*
SC 95 185-313-0	4A	M1	29.8	18.6	160.2150538	L	*U. spelaeus*
SC 95 204-326-0	4A	M1	29.2	20.8	140.3846154	L	*U. spelaeus*
SC 95 231 -457-0	4A	M1	27.3	18	151.6666667	R	*U. spelaeus*
SC 95 375-107-4	4A	M1	28.7	20.3	141.3793103	L	*U. spelaeus*
SC 95 376-0-1	4A	M1	27	18.4	146.7391304	R	*U. spelaeus*
SC 95 391-186-0	4A	M1	27.1	19.9	136.1809045	R	*U. spelaeus*
SC 97 113-395-9	4A	M1	30.5	21.7	140.5529954	L	*U. spelaeus*
SC 97 391-201-8	4A	M1	28.1	18.8	149.4680851	L	*U. spelaeus*
SC 97 57-195-0	4A	M1	23.3	17	137.0588235	L	*U. spelaeus*
SC 99 38-641-0	4A	M1	29.8	20.8	143.2692308	L	*U. spelaeus*
SC 91 599-0-6	4A	M1	28.8	19	151.5789474	R	*U. spelaeus*

SC 88 92-0-3	3	M2	49.31	25.19	195.7522827	L	*U. spelaeus*
SC 90 61-0-4	3	M2	45.6	22.55	202.2172949	L	*U. spelaeus*
SC 92 440-0-9	3	M2	48.8	24.97	195.4345214	L	*U. spelaeus*
SC 93 163-0-15	3	M2	42.55	21.05	202.1377672	L	*U. spelaeus*
SC 93 163-0-9	3	M2	42.6	23.4	182.0512821	R	*U. spelaeus*
SC 94 46-0-3	3	M2	48.92	24.43	200.2455997	L	*U. spelaeus*
SC 94 524 -0-82	3	M2	49.14	24.52	200.4078303	L	*U. spelaeus*
SC 94 71-0-18	3	M2	44.74	23.94	186.8838764	R	*U. spelaeus*
SC 92 434-0-8	3	M2	46.67	23.59	197.838067	R	*U. spelaeus*
SC 92 445-0-2	3	M2	43.29	22.3	194.1255605	L	*U. spelaeus*
SC 92 445-0-3	3	M2	40.79	21.09	193.4091987	R	*U. spelaeus*
SC 93 322-0-6	3	M2	40.28	20.88	192.9118774	L	*U. spelaeus*

SC 93 327-0-7	3	M2	46.64	23.46	198.8064791	R	*U. spelaeus*
SC 94 495-3-2	3	M2	45.57	23.59	193.1750742	L	*U. spelaeus*
SC 94 515-0-74	3	M2	41.02	22.95	178.7363834	R	*U. spelaeus*
SC 95 41-19-18	3	M2	45.1	24.09	187.2146119	R	*U. spelaeus*
SC 00 123-21-0	3	M2	43.77	22.88	191.3024476	R	*U. spelaeus*
SC 81 44-0-939	3	M2	44.93	22.16	202.7527076	L	*U. spelaeus*
SC 83 152-0-880	3	M2	44.16	23.76	185.8585859	R	*U. spelaeus*
SC 83 152-0-863	3	M2	47.58	22.26	213.7466307	R	*U. spelaeus*
SC 85 121-0-853	3	M2	45.94	23.01	199.6523251	R	*U. spelaeus*
SC 86 132-0-908	3	M2	47.24	23.78	198.6543314	R	*U. spelaeus*
SC 86 135-0-899	3	M2	48.1	23.38	205.7313944	L	*U. spelaeus*
SC 86 3-0-919	3	M2	49.5	24.22	204.3765483	L	*U. spelaeus*
SC 87 138-0-910	3	M2	43.76	22.7	192.7753304	R	*U. spelaeus*
SC 87 81-0-878	3	M2	50.55	24.46	206.6639411	R	*U. spelaeus*
SC 89 118-0-858	3	M2	47.91	25.04	191.3338658	L	*U. spelaeus*
SC 89 145-0-864	3	M2	46.16	23.84	193.6241611	R	*U. spelaeus*
SC 90 73-0-78	3	M2	43.8	21.54	203.3426184	R	*U. spelaeus*
SC 91 213-0-862	3	M2	44.79	23.34	191.9023136	L	*U. spelaeus*
SC 91 379-0-869	3	M2	47.45	23.2	204.5258621	L	*U. spelaeus*
SC 91 39-0-872	3	M2	47.33	23.88	198.19933	R	*U. spelaeus*
SC 92 111-0-937	3	M2	45.42	21.96	206.8306011	R	*U. spelaeus*
SC 92 150 -0-4315	3	M2	40.16	22.96	174.912892	R	*U. spelaeus*
SC 92 386-0-935	3	M2	49.09	24.45	200.7770961	R	*U. spelaeus*
SC 92 399-0-865	3	M2	40.91	21.3	192.0657277	R	*U. spelaeus*
SC 92 407-0-997	3	M2	47.6	24.28	196.0461285	R	*U. spelaeus*
SC 92 452-0-938	3	M2	43.81	23.55	186.029724	R	*U. spelaeus*
SC 92 458-0-862	3	M2	43.83	22.82	192.0683611	R	*U. spelaeus*
SC 94 405-0-902	3	M2	45.29	23.24	194.8795181	L	*U. spelaeus*
SC 94 435-0-875	3	M2	44.3	23.15	191.3606911	R	*U. spelaeus*
SC 94 435-0-894	3	M2	45.86	23.36	196.3184932	L	*U. spelaeus*
SC 95 475-0-944	1A	M2	42.1	21.1	199.5260664	L	*U. spelaeus*
SC 95 488-0-82	1A	M2	46.5	23.4	198.7179487	R	*U. spelaeus*
SC 01 56-102-0	1A	M2	48.7	23.2	209.9137931	R	*U. spelaeus*
SC 01 80-0-30	1A	M2	48.8	25.2	193.6507937	L	*U. spelaeus*
SC 82 133-0-913	1A	M2	45.8	23.2	197.4137931	R	*U. spelaeus*
SC 82 143-0-860	1A	M2	44.7	24	186.25	R	*U. spelaeus*
SC 83 108-0-914	1A	M2	48.2	23.9	201.6736402	R	*U. spelaeus*
SC 83 152-0-860	1A	M2	46.7	22.6	206.6371681	R	*U. spelaeus*
SC 85 151-0-4659	1A	M2	46.1	25.1	183.6653386	L	*U. spelaeus*
SC 85 173-0-883	1A	M2	46	24.5	187.755102	L	*U. spelaeus*
SC 86 131-0-923	1A	M2	45.8	23.3	196.5665236	L	*U. spelaeus*
SC 86 131-0-900	1A	M2	47.8	23.5	203.4042553	R	*U. spelaeus*
SC 86 21-0-905	1A	M2	47.3	23	205.6521739	R	*U. spelaeus*

SC 86 21-0-916	1A	M2	45.5	22.4	203.125	R	*U. spelaeus*
SC 87 139-0-882	1A	M2	41.6	24	173.3333333	R	*U. spelaeus*
SC 87 42-0-81	1A	M2	48.1	26	185	L	*U. spelaeus*
SC 88 6-0-931	1A	M2	42.4	22	192.7272727	L	*U. spelaeus*
SC 90 73-0-80	1A	M2	46.1	23.6	195.3389831	R	*U. spelaeus*
SC 91 173-0-936	1A	M2	49.7	26.7	186.1423221	R	*U. spelaeus*
SC 91 173-0-926	1A	M2	41.4	22.7	182.3788546	L	*U. spelaeus*
SC 91 239-0-881	1A	M2	47	26	180.7692308	L	*U. spelaeus*
SC 91 41-0-934	1A	M2	46.3	22.7	203.9647577	R	*U. spelaeus*
SC 91 78-0-912	1A	M2	48.8	23.6	206.779661	R	*U. spelaeus*
SC 92 115-0-996	1A	M2	41.6	21.4	194.3925234	L	*U. spelaeus*
SC 92 153-0-995	1A	M2	47.6	25.4	187.4015748	R	*U. spelaeus*
SC 92 170-0-873	1A	M2	44.8	22.4	200	L	*U. spelaeus*
SC 92 182-0-898	1A	M2	44	22.2	198.1981982	R	*U. spelaeus*
SC 92 394-0-4314	1A	M2	43.2	21.8	198.1651376	L	*U. spelaeus*
SC 94 433-0-79	1A	M2	44.4	24.3	182.7160494	L	*U. spelaeus*
SC 95 496-0-893	1A	M2	44.8	22.4	200	R	*U. spelaeus*
SC 95 539-0-941	1A	M2	45.8	24	190.8333333	R	*U. spelaeus*
SC 89 135-0-885	1A	M2	50.7	24.1	210.373444	R	*U. spelaeus*
SC 97 37 -0-149	1A	M2	52.6	25.8	203.875969	L	*U. spelaeus*
SC 99 66-0-905	1A	M2	47.5	23.5	202.1276596	R	*U. spelaeus*
SC 92 422-0-4	1A	M2	44	22.1	199.0950226	L	*U. spelaeus*
SC 95 102-0-124	1A	M2	43.6	22.6	192.920354	L	*U. spelaeus*
SC 95 419-0-51	1A	M2	49	26.5	184.9056604	R	*U. spelaeus*
SC 95 442-0-11	1A	M2	43.4	23	188.6956522	R	*U. spelaeus*
SC 95 468-0-68	1A	M2	47	24.6	191.0569106	L	*U. spelaeus*
SC 96 212-66-8	1A	M2	50.1	25.5	196.4705882	R	*U. spelaeus*
SC 96 230-61-1	1A	M2	48.5	23.8	203.7815126	L	*U. spelaeus*
SC 82 230-0-2	1A	M2	47.7	24.1	197.9253112	R	*U. spelaeus*
SC 82 237-0-9	1A	M2	43.8	21.4	204.6728972	R	*U. spelaeus*
SC 89 73-0-4	1A	M2	45.9	23.2	197.8448276	R	*U. spelaeus*
SC 90 80-0-5	1A	M2	45.2	24.5	184.4897959	L	*U. spelaeus*
SC 91 460-0-9	1A	M2	48.5	23.6	205.5084746	R	*U. spelaeus*
SC 91 537-0-8	1A	M2	48.2	23.9	201.6736402	L	*U. spelaeus*
SC 90 173-0-3	1A	M2	47.5	23.3	203.8626609	L	*U. spelaeus*
SC 91 422-0-10	1A	M2	48.3	23.5	205.5319149	L	*U. spelaeus*
SC 91 432-0-6	1A	M2	46.5	22.8	203.9473684	L	*U. spelaeus*
SC 91 531-0-9	1A	M2	46.4	22	210.9090909	L	*U. spelaeus*
SC 92 532-0-3	1A	M2	43.5	21.3	204.2253521	R	*U. spelaeus*
SC 95 36-41-18	1A	M2	48.1	23.7	202.9535865	L	*U. spelaeus*
SC 98 358-0-393	1A	M2	47.9	25.1	190.8366534	L	*U. spelaeus*
SC 92 1280-0-5	1A	M2	45.4	23.8	190.7563025	L	*U. spelaeus*
SC 91 570-0-3	1A	M2	47.3	25.2	187.6984127	L	*U. spelaeus*

SC 92 1280-71-1	1A	M2	42.6	22.3	191.0313901	R	*U. spelaeus*
SC 92 507-0-15	1A	M2	45.6	23.4	194.8717949	R	*U. spelaeus*
SC 00 131-814-59	4A	M2	43.9	23	190.8695652	L	*U. spelaeus*
SC 83 109-0-1933	4A	M2	39.8	19.5	204.1025641	L	*U. spelaeus*
SC 86 62-0-2184	4A	M2	45	21.9	205.4794521	R	*U. spelaeus*
SC 90 113-0-2189	4A	M2	40.2	20.5	196.097561	R	*U. spelaeus*
SC 91 616-0-12	4A	M2	42.3	21.1	200.4739336	R	*U. spelaeus*
SC 94 439-118-0	4A	M2	46.1	22.3	206.7264574	L	*U. spelaeus*
SC 95 172-53-0	4A	M2	46.3	23.7	195.3586498	R	*U. spelaeus*
SC 95 185-299-0	4A	M2	48.1	23.8	202.1008403	R	*U. spelaeus*
SC 95 382-168-0	4A	M2	45.8	23.1	198.2683983	L	*U. spelaeus*
SC 95 478-111-0	4A	M2	40.5	22.5	180	R	*U. spelaeus*
SC 96 113-95-0	4A	M2	46	23	200	R	*U. spelaeus*
SC 96 277-176-0	4A	M2	42	21.4	196.2616822	R	*U. spelaeus*
SC 97 129-481-0	4A	M2	41.5	21.5	193.0232558	R	*U. spelaeus*
SC 98 190-270-0	4A	M2	47.5	23.5	202.1276596	R	*U. spelaeus*
SC 98 286-277-0	4A	M2	44.6	23.5	189.787234	L	*U. spelaeus*
SC 98 317-376-0	4A	M2	40.5	21.9	184.9315068	R	*U. spelaeus*
SC 83 63 -0-2190	4A	M2	42	22.3	188.3408072	R	*U. spelaeus*
SC 83 66-0-2193	4A	M2	38.6	20.3	190.1477833	R	*U. spelaeus*
SC 86 33-0-2188	4A	M2	39.2	20.9	187.5598086	R	*U. spelaeus*
SC 89 10-0-2192	4A	M2	46	24	191.6666667	L	*U. spelaeus*
SC 89 83-0-2187	4A	M2	37.9	21.2	178.7735849	L	*U. spelaeus*
SC 90 78-0-4	4A	M2	40.6	21.4	189.7196262	R	*U. spelaeus*
SC 91 574-0-2	4A	M2	45.5	23.5	193.6170213	L	*U. spelaeus*
SC 91 589-0-5	4A	M2	47.8	23	207.826087	L	*U. spelaeus*
SC 91 597-0-1	4A	M2	46.9	23.3	201.2875536	L	*U. spelaeus*
SC 91 606-0-1	4A	M2	47	21.8	215.5963303	L	*U. spelaeus*
SC 91 616-0-6	4A	M2	45.7	22.7	201.3215859	L	*U. spelaeus*
SC 92 6-0-8	4A	M2	43.5	23.3	186.695279	L	*U. spelaeus*
SC 94 305-254-0	4A	M2	38	19.7	192.893401	L	*U. spelaeus*
SC 94 401-97-0	4A	M2	44.9	23.1	194.3722944	L	*U. spelaeus*
SC 95 178-81-0	4A	M2	44.5	24.8	179.4354839	L	*U. spelaeus*
SC 98 326 -1-0	4A	M2	45.1	22.9	196.9432314	R	*U. spelaeus*
SC 99 80-66-0	4A	M2	46.5	23.9	194.5606695	R	*U. spelaeus*